



## Juvenile rough-and-tumble play predicts adult sexual behaviour in American mink



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The existence of play, a form of behaviour without obvious benefits to survival or reproduction, is a long-standing ethological mystery. Experiments in which socially deprived juvenile male mammals develop into sexually incompetent adults, along with widespread sexual dimorphism in rough-and-tumble play (R&T), suggest that R&T may prepare juvenile males for adult sexual behaviour. To test this hypothesis, we conducted a longitudinal study of American mink, *Neovison vison*, on two farms, with two cohorts each. For males ( $N = 121$ ), we predicted that individuals with the highest frequencies of rough-and-tumble play as juveniles (10–20 weeks old) would, as adults, show shorter latencies to bite females' necks and to begin copulating, and copulate for longer durations. On one farm, we conducted a pilot study of females ( $N = 10$ ) as a preliminary test of the hypothesis that R&T also prepares females for adult sexual behaviour. Here, our predictions were the opposite of those for males, since abilities to limit the number or duration of copulations could allow females to exercise pre- or postcopulatory mate choice. In total, we observed 1669 male–female encounters and 1004 separate copulations. As predicted, frequent juvenile R&T predicted long-lasting copulations in adult males and longer latencies to copulate in adult females. This was true specifically of rough-and-tumble play itself, independently of general activity levels and, among a subset of 32 males reared in environmentally enriched housing, also independently of solitary object play. To our knowledge, this is the first demonstration that juvenile rough-and-tumble play predicts adult sexual behaviour in any species. Further research is required to test whether our results for females can be replicated, and, importantly, to determine whether play truly has a causal role in either of these correlational relationships.

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Play is widespread in young mammals, despite providing no obvious benefits to survival or reproduction. Complicating matters for ethologists interested in its potential functions: play has proven hard to manipulate experimentally in a specific way (Ahloy Dallaire, 2015); any benefits it has may differ between species and/or play subtypes (e.g. Burghardt, 2005; Fabri, 1983; Smith, 1982); and it could even have evolved as a nonadaptive by-product of other beneficial traits (Burghardt, 2005, 2014). Our focus here is 'rough-and-tumble' play (R&T), commonly known as play fighting, which has been hypothesized to play an important role in the development of male sexual behaviour (Beach, 1967; Missakian, 1972; Twigg, Popolow, & Gerall, 1978; reviewed in; Pellis & Pellis, 2009). Evidence for this hypothesis is distinctly

mixed. As would be expected if R&T has sexually dimorphic fitness benefits, males typically engage in more R&T than females, particularly in promiscuous or polygynous species (Chau, Stone, Mendoza, & Bales, 2008). The body parts targeted in play and later sexual behaviour are also often the same, and there can exist parallel sexual dimorphism in the manoeuvres performed in R&T and in sexual behaviour (Pellis & Bell, 2011; Pellis & Pellis, 1990, 2009; Smith, Forgie, & Pellis, 1998). Thus, R&T could serve to practise components of male courtship and mating, although counter to this idea, potentially presexual manoeuvres seen in juvenile rat R&T do not seem to improve with experience (Himmeler et al., 2015). Furthermore, socially isolated juvenile males, deprived of R&T, typically show impairments in sexual behaviour as adults (reviewed in Pellis & Pellis, 2009). These can be reduced or even avoided by allowing isolates just one brief daily peer interaction session (Beach, 1967; Hole, Eimon, & Plotkin, 1986; Zimbardo, 1958), which they typically devote almost entirely to R&T (Eimon, Morgan, & Kibbler, 1978). Other experiments, however, suggest that play is not crucial: juvenile males may develop normal sexual

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behaviour despite being housed with nonplayful adults or permitted only limited nonplay contact (through a mesh partition) with other juveniles (Cooke & Shukla, 2011; Gruendel & Arnold, 1969; Hole et al., 1986). This equivocal picture likely reflects the difficulty of manipulating R&T without affecting other types of social behaviour in deprivation studies.

The American mink, *Neovison vison*, is potentially an excellent model in which to study the hypothesis that R&T plays a role in the development of male sexual behaviour. Bred by the thousands on commercial farms (e.g. Mason et al., 2013), they retain many characteristics of their wild counterparts, such as pronounced sexual dimorphism, induced ovulation and delayed implantation, and annual reproductive cycles involving promiscuous, oftentimes violent copulations (Adams, 1981; Dunstone, 1993; Enders, 1952). If released from captivity, they readily establish feral populations (Dunstone, 1993) and interbreed with wild conspecifics (Kidd, Bowman, Lesbarrères, & Schulte-Hostedde, 2009). Experimental studies have also shown that R&T is their primary form of play (Vinke, van Leeuwen, & Spruijt, 2005); that during this behaviour, juveniles often attack and bite each other's necks (Jonasen, 1987; Poole, 1978), as adult males do when mating (Dunstone, 1993; Kuby, 1982, cited in; Vinke et al., 2005); that juveniles produce a 'chuckle' vocalization during play that is at least superficially similar to adult mating vocalizations (Enders, 1952; Gilbert, 1969; MacLennan & Bailey, 1969); and that males socially isolated before 8 weeks of age, the start of an age-related peak in R&T (Hansen, Houbak, & Malmkvist, 1997; Vinke et al., 2005), show long-term increases in abnormal behaviour (e.g. Mason, 1994) and generally fail to copulate in adulthood (Bassett, Travis, Abernathy, & Warner, 1959; Gilbert & Bailey, 1969; Hansen et al., 1997) for reasons that include failing to obtain the proper grip on potential mates' napes (Eibl-Eibesfeldt, 1982, 1963; Gilbert & Bailey, 1969). Using a longitudinal approach and large sample sizes, and exploiting naturally occurring variation between individuals in levels of R&T, we therefore studied farmed mink to test correlational predictions of the hypothesis that juvenile rough-and-tumble play prepares males for adult sexual behaviour. Of course, correlations between juvenile play behaviour and adult sexual behaviour or other longitudinal outcomes cannot provide unequivocal evidence for beneficial effects of play: any such effects could be mediated by unobserved variables (Fagen & Fagen, 2004, 2009); and there may be no correlations even where benefits do exist, if only a very small amount of play experience is enough to develop normal adult behaviour, or if each individual plays the minimum amount required to reach adequate sexual performance as an adult (Martin & Caro, 1985). That being said, correlations would be expected if juvenile play has graded effects on sexual behaviour, such that greater amounts of play confer stronger benefits. Such enhanced sexual competence could potentially allow male mink to overcome the physical resistance shown by females at all steps of courtship and mating: they fight to prevent males from biting their napes, a prerequisite for intromission, and then repeatedly struggle to escape during copulation itself (Dunstone, 1993; Enders, 1952). For male mink, we therefore predicted that if R&T has graded and positive effects on sexual behaviour, then frequent juvenile R&T would be associated in adulthood with short latencies to bite females' napes and to begin copulating, and with long copulation durations. We further predicted that these effects would be specific to R&T, and not manifest with respect to other types of play.

The potential relationship between R&T and female sexual behaviour is harder to make directional predictions for. Positive links between female fertility and aspects of R&T have been identified in ground squirrels (*Urocitellus beldingi*; Nunes, 2014) and rats (Parent, Del Corpo, Cameron, & Meaney, 2013), but these seemed to

be mediated by competitive interactions between females, and sexual behaviour itself was not examined. Furthermore, socially isolating juvenile females has produced mixed results. In some species, isolates reportedly either become less receptive (Harlow, Dodsworth, & Harlow, 1965; Mitchell, Raymond, Ruppenthal, & Harlow, 1966) or develop roughly normal sexual behaviour (Hole et al., 1986; Rogers & Davenport, 1969). In contrast with some of these results and with those seen in male mink, female mink isolated before 8 weeks of age mate more readily as adults, an effect linked with reduced aggression towards males (Gilbert & Bailey, 1969). Such effects may reflect the rather violent courtship and mating of mink, noted above. While females in mate choice experiments mate multiply and voluntarily approach males, they actively resist and sometimes avoid copulation, and also show distinct preferences for some males over others, copulating more often or for longer durations with particular phenotypes (Diez-León et al., 2013; Thom, Macdonald, Mason, Pedersen, & Johnson, 2004). Thus, females likely use aggressive pre-coital and coital behaviour to promote fertilization by preferred males (Enders, 1952; Fleming, 1996). If R&T prepares females for the physical struggles involved in mating, then it may allow them to exercise a greater degree of pre- and/or postcopulatory mate choice (Andersson & Simmons, 2006; Fleming, 1996; Larivière & Ferguson, 2003). In our longitudinal study, we therefore also followed a smaller pilot sample of juvenile females into adulthood, cautiously predicting that frequent juvenile R&T would be associated with longer latencies to be bitten and mated by males, and with shorter copulation durations.

## METHODS

This research was approved by the University of Guelph's Animal Care Committee (protocol numbers AUP 10R108 and eAUP 1435) in compliance with Canadian Council on Animal Care guidelines. Animal housing and husbandry conformed to the requirements of the Canada Mink Breeders Association and the National Farm Animal Care Council (National Farm Animal Care Council, 2013).

### Juvenile Period

#### Subjects and housing

We studied two cohorts of American mink per farm on each of two commercial fur farms in Ontario, Canada (hereafter 'Farm A' and 'Farm B', corresponding to names used previously by Meagher et al., 2014). Subjects were transferred from weanling groups to pair housing at about 8–10 weeks of age, in late June or early July. Pairs were housed in semi-enclosed barns, under natural lighting, in 61 × 30 × 46 cm (L × W × H) wire cages furnished with an elevated nestbox. Half of the Farm A, Cohort 1 pairs were additionally provided with a golf ball, a perforated plastic 'whiffle' ball and a hanging length of hose as part of a separate experiment on environmental enrichment (Meagher et al., 2014). All pairs comprised one male and one female, with the exception of some male–male pairs in Farm A, Cohort 2. Farmers fed juveniles a standard meat-based paste in the afternoon and, on Farm A, also in the morning. We used several colour types: strains selected for their fur colour. All Farm A subjects were of the black colour type, while Farm B included both black and 'paste' (beige) mink housed in mixed- or same-colour pairs, as well as, in the second cohort, pairs of 'demi' (dark brown) mink.

#### Behavioural observation

We observed juvenile behaviour in pair housing between July and September, over all daylight hours, starting 1 h after sunrise

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